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The feasibility of bomb radiocarbon analysis to support an age-at-length relationship for red abalone, Haliotis rufescens Swainson in northern California

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Bomb ^{14}C and red abalone age and growth

Abstract: Analysis of bomb generated radiocarbon (^{14}C) changes in a red abalone, *Haliotis rufescens* Swainson shell was used to investigate age-at-length relationships derived from data from a previous multi-year, multi-site tag-recapture study. Shell carbonate was extracted from four successive growth trajectory locations in a single shell with a length of 251 mm MSL. Extraction locations were based on VBGF predictions and chosen to span the initial rise of the ^{14}C-bomb pulse that is known to have occurred in surface ocean waters during 1958 ± 1 y in the northeast Pacific. The close temporal correspondence of the red abalone sample series to regional $\Delta^{14}C$ records demonstrated the utility of the technique for validating age-at-length relationships for the red abalone. The findings provided support for a mean VBGF derived age of 32 y (range 30 to 33 y) for the specimen; however, the analysis of ^{14}C data indicated that the specimen could be older.

Key Words: accelerator mass spectrometry, carbon-14, von Bertalanffy growth function, Haliotidae

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INTRODUCTION

The red abalone, *Haliotis rufescens* Swainson, supports an important recreational fishery in northern California and was once important commercially (Karpov et al. 2000). Because of historical depletions of *Haliotis* spp. populations in California (Karpov et al. 2000, Rogers-Bennett et al. 2002) there are concerns about the sustainability of the current fishery (California Department of Fish and Game, Marine Region 2005). Biological information, such as the age-at-length relationship, is a key parameter for the determination of management strategies and has only recently been described for red abalone in northern California by analysis of marked and recaptured individuals (Rogers-Bennett et al. 2007).

Although mark-recapture studies provide information about the age-at-length relationship, they can be limited in their ability to estimate the ages of large individuals. Age-at-length studies of northern California red abalone raised in aquaria indicate that the average size of the largest individuals in the population (L_∞) would be 170 to 236 mm MSL (maximum shell length) (Ault 1985). Rogers-Bennett et al. (2007) reported L_∞ values of 254.2 mm MSL from individuals marked and recaptured at one site in northern California. However, red abalone exhibit asymptotic growth with a maximum recorded size of 313 mm MSL (Rogers-Bennett et al. 2007) and it is not uncommon for the lengths of individuals targeted in the recreational fishery to exceed the

published L_∞ values. Thus, it is not possible to use reported age-at-length relationships to estimate the ages for a component of the harvested population.

Methods that enable the determination of the ages of large individuals are necessary for the complete description of the age-at-length relationship of a species. Two strategies for directly estimating age-at-length for abalone are counting growth zones (discontinuous rings, marks, or lines in the shell) and analysis of seasonal stable isotope ratios in shell carbonate. Use of growth zone counts for age determination can be problematic: it has been documented that the formation of growth zones are irregular and may preclude consistent quantification (Forster 1967, Poore 1970, McShane & Smith 1992). Age estimation based on the ratio of stable isotopes in shell carbonate was successful at determining age and growth rates for a few mollusk species, including abalone (Cespuglio et al. 1999, Richardson 2000, Gurney et al. 2005). Oxygen isotopes are incorporated into shell carbonates in equilibrium with seawater and oxygen isotope ratios ($^{18}O/^{16}O$) can be correlated with temperature, thereby providing a measure of temperature change as a proxy for seasonal change (Epstein et al. 1953). In addition, changes in the ratio of stable carbon isotopes ($^{13}C/^{12}C$) can also provide a proxy for rate of shell formation by creating a record of seasonal productivity (Fairbanks & Dodge 1979, Krantz et al. 1984, Romanek et al 1987). The accuracy of these stable isotope methods for age determination is contingent upon the assumption that patterns in isotopic ratio change are indicative of annual growth. Analysis of stable isotopes has proven useful for determining early growth rates in ontogeny when growth rates are greatest, but the method is limited by the resolution of carbonate extraction techniques and cannot be performed at a resolution necessary to detect seasonal patterns in the older, slower growing parts of the shell (Romanek et al. 1987). Because of these limitations and assumptions, an independent chronometer for shell carbonate formation is desirable for accurate age and growth determination.

The use of the time-specific bomb-radiocarbon (^{14}C) marker preserved in the carbonate structure of organisms is a promising method for validating age-at-length estimates (Campana 2001). Atmospheric testing of thermonuclear devices in the 1950s and 1960s greatly increased the naturally occurring levels of ^{14}C in the atmosphere. Atmosphere-ocean gas exchange processes transferred bomb-derived ^{14}C into the surface oceans and it was subsequently taken up and preserved in the carbonate structures of marine organisms residing in the mixed layer. Identification of the initial rise in bomb ^{14}C in the carbonate structure of these organisms provides a chronological tool for determining age and growth. Successful applications of this technique range from validation of growth-zone derived estimates for invertebrates (Turekian et al. 1982, Weidman & Jones 1993) and fishes (Kalish 1993, Kerr et al. 2004, Piner & Wischniowski 2004) to the determination of growth rates and age when growth-zone derived age estimates were poor or not possible for invertebrates (Landman et al. 1988, Ebert & Southon 2003), algae (Frantz et al. 2000, 2005), and fishes (Andrews et al. 2005). In this study, a series of carbonate samples taken along the trajectory of growth from a single red abalone shell were analyzed for ^{14}C to investigate the feasibility of using the time-specific bomb ^{14}C marker to validate a red abalone age-at-length relationship.

METHODS

One red abalone shell (251 mm MSL) was used in this study to investigate the feasibility of detecting $\Delta^{14}C$ in red abalone shell and to assess the validity of competing VBGF estimates using the change in ^{14}C due to atmospheric nuclear weapons testing ($\Delta^{14}C$) recorded in shell material. The specimen analyzed in this study was collected in 1968, with an uncertainty of $\pm$ 1 y, from near the Gualala River, Mendocino, in northern California, USA. To prepare the shell for carbonate

extraction thin sections (approximately 2 mm wide) were removed perpendicular to the growth margin in multiple locations using a diamond bladed saw. Thin sections were mounted on glass slides with Cytoseal™ or wax. Four carbonate samples were extracted from the prismatic layer of the mounted thin sections using a New Wave® micromill with a 0.5 mm Brassler® drill bit. Extraction locations were based on preliminary VBGF predictions, described below, and were chosen to span the initial rise of the ^{14}C-bomb pulse that is known to have occurred in surface ocean waters at 1958 ± 1. Because extractions from a single individual are necessarily autocorrelated we refer to each as a subsample. The first subsample was taken at 249 mm MSL, within 2 mm of the leading margin of growth, and three additional subsamples were taken at 227 mm, 217 mm, and 75 mm MSL. The precision of extraction was ± 0.5 mm of the target sample location.

The extraction procedure produced small powdered fragments (~ 5 mg) that were weighed to the nearest 0.1 mg. For $\Delta^{14}C$ analysis, calcium carbonate ($CaCO_3$) was converted to CO_2 and then to graphite (Vogel 1987) and measured for ^{14}C content by accelerator mass spectrometry (AMS) at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, Livermore, California, USA. The ^{14}C measurements were reported as $\Delta^{14}C$ values and an assumed $\delta^{13}C$ value of zero was used in calculating the $\Delta^{14}C$ values, which is representative of marine carbonates (Stuiver & Polach 1977). We tested for ^{14}C contamination of the shell specimen and the workspace where carbonate extractions were performed. Alcohol soaked filter paper was rubbed on the shell and equipment ($n = 4$). No ^{14}C contamination was detected on any equipment or the shell specimen.

To estimate the dates of formation of extracted subsamples, three VBGF models were constructed based on tag-recapture data from northern California. These data were obtained from

899 tagged and recaptured red abalone at five sites in Sonoma and Mendocino counties from 1971 to 1978 (for details see Leaf et al. 2007). Only tagged red abalone at liberty for 1 y ± 18 days (~ 5% of 1 y) within single or multiple year intervals were used for analysis. Individuals at liberty for a greater or lesser time period were excluded from VBGF parameter estimation because we suspected that growth for this species is not uniform throughout the year. Fabens' (1965) method was used to derive the VBGF parameter k, the growth rate constant, y^{-1}, and three L_∞ values, the average maximum size of an individual in the population (mm MSL), from the tag-recapture data using a non-linear curve fitting protocol in R (version 2.3.1).

$$L_{recapture} = L_{tag} + (L_\infty - L_{tag})(1 - e^{(-k*\Delta t)}) \qquad \text{Eq. 1}$$

The value of L_∞ was fixed in each of the three VBGF models to the maximum recorded size of the species (313 mm MSL) and two arbitrarily chosen sizes: 298 mm MSL and 283 mm MSL. Variables in the Fabens' equation (Eq. 1) are: $L_{recapture}$, the MSL (mm) of an individual at the time of recapture; L_{tag}, the MSL (mm) of an individual at the time of tagging; and Δt, the duration at liberty in years. In this formulation of the VBGF we assume that the age at size 0 mm (t_0) is 0 y. A Ford-Walford plot (Walford 1946) was used to estimate k from the tag-recapture data to parameterize the non-linear curve-fitting algorithm. Confidence intervals (95%) of the mean value of k for each of the three candidate VBFG models were determined by Monte-Carlo sampling of randomized residual error values. The three von Bertalanffy growth functions were evaluated for goodness of fit by Akaike information criteria (AIC) and qualitatively to tag-recapture data using the growth vector method presented by Cailliet et al. (1992). AIC is a measure of the goodness of fit of competing models to data. The value Δ_i is a measure of the fit of a model, model i, relative to that of the best fit model (the model with the lowest AIC value, AIC_{min}) where $\Delta_i = AIC_i - AIC_{min}$ (Burnham & Anderson 2002). Values of $\Delta_i > 10$ indicate that the competing model has very little

support (Burnham & Anderson 2002). Growth vector analysis of the tag-recapture data was performed by anchoring growth vectors to the VBGF by assuming that the length at first capture corresponds to the age predicted by the VBGF. Growth vectors represent the change in time since first capture (Δt, y) and the change in length during the time at liberty (ΔL, mm).

For each subsample extracted from the shell the back-calculated mean and range of the date of shell formation were determined based on estimates of growth from each of the three VBGF growth models. The range of the date of shell formation was calculated using the confidence interval associated with *k* from the VBGF, the incorporation of the uncertainty of the year of shell collection (1968 $\pm$ 1 y), and the incorporation of the width of the subsample extraction ($\pm$ 0.5 mm). Thus, the estimate of the earliest date of shell formation at each of the four subsample target locations, was estimated using the upper 95% confidence interval of *k*, an assumed date of shell collection of 1967, and a shell length given that the MSL is the minimum length sampled during extraction (subsample target – 0.5 mm). The estimate of the most recent date of shell formation at each of the four subsample locations area was estimated using a small *k* value (the lower 95% confidence interval), an assumed collection year of 1969, and a shell length given that the MSL is the maximum length sampled during extraction (subsample target + 0.5 mm). The mean year of shell formation at a target area was estimated using the mean value of *k*, the median collection year of 1968, and the MSL at the target extraction point.

The fit of the candidate VBGF model estimates of the dates of shell subsample formation were evaluated qualitatively and through simulation. The estimate of the date of formation from each VBGF estimate of each subsample was compared with the Δ^{14}C records for two regional reference Δ^{14}C time series: yelloweye rockfish (*Sebastes ruberrimus*) (Kerr et al. 2004) and Pacific halibut (*Hippoglossus stenolepis*) (Piner & Wischniowski 2004). The temporal agreement

of the red abalone subsample series with these records were used as one basis for evaluation of the age and growth estimates from each of the VBGF trajectories. A simulation was also performed in which the precision of the three VBGF models to correctly predict the year of formation of the subsample formed at the inception of the radiocarbon rise was evaluated.

RESULTS

The quality of each of the VBGF models to describe growth based on the tag-recapture data was variable. The VBGF, with a constrained L_∞ value of 313 mm MSL had a poor fit to the tag-recapture data ($\Delta_i = 61.3$) relative to other models. This model had an estimate of k that indicated that growth ($k = 0.0561$ y $^{-1}$, 95% CI: 0.0532 to 0.0589 y $^{-1}$) was less than half that predicted from the Ford-Walford estimate ($k = 0.137$ y^{-1}). The estimate of k increased in models with smaller L_∞ values and model fit was improved: the model with $L_\infty = 298$ mm MSL had an estimated $k =$ 0.0619 y^{-1} (95% CI: 0.0618 to 0.0647 y $^{-1}$) and the fit to the data was improved ($\Delta_i = 32.8$). The von Bertalanffy growth estimate with an L_∞ value of 283 mm MSL had the best fit to the tag-recapture data (AIC = 5864.2) and was predicted to have the greatest growth rate, $k = 0.0689$ y^{-1} (95% CI: 0.0673 to 0.0705 y^{-1}). This best fit model resulted in a predicted age of the specimen to be 32 y with a range of 30 to 33 y. The distribution of observed growth, represented by the growth vectors, relative to the growth predicted by the VBGF for the best fit model, indicated that the predicted VBGF model underestimated growth of individuals smaller than 150 mm and overestimated growth of individuals larger than 150 mm (Figure 2). This pattern in the growth vectors was evident for each of the other candidate VBGF models.

There was a correspondence between the Δ^{14}C values and VBGF age estimates from the red abalone specimen with each of the Δ^{14}C reference time series' (Figure 1). The only red

abalone subsample with a clearly post-bomb $\Delta^{14}C$ level was from the 249 mm MSL subsample ($\Delta^{14}C‰ = -16.8‰ \pm 4.8$) (Table 1). This subsample had an estimated year of formation of 1966 to 1968, based on the three VBGF models, and had $\Delta^{14}C$ values similar to yelloweye rockfish samples with estimated years of formation of 1964 ($\Delta^{14}C‰ = -22 \pm 3$) and 1965 ($\Delta^{14}C‰ = -7.4 \pm 3.1$). The subsample extracted at the 227 mm MSL location ($\Delta^{14}C‰ = -93.2 \pm 4.2$) was estimated to have been formed during the inception of the rise of the radiocarbon concentration in the northeastern Pacific (1959 to 1962) based on the three VBGF estimates (Table 1). The $\Delta^{14}C‰$ value of this subsample was similar to samples from yelloweye rockfish with estimated years of formation of 1950 to 1963 and Pacific halibut samples estimated to have been formed in 1944 to 1958. The subsample taken from the 217 mm MSL location ($\Delta^{14}C‰ = -104.0 \pm 3.6$) had an estimated year of formation, based on VBGF estimates, of 1957 to 1960 (Table 1). The subsample extracted from the 217 mm MSL location had $\Delta^{14}C‰$ that were most similar to samples from the yelloweye rockfish estimated to be formed in 1944 ± 2 y and 1956 ± 2 y and six samples from the Pacific halibut time series with estimated years of formation of 1947 to 1959. The subsample extracted from the 75 mm MSL location ($\Delta^{14}C‰ = -115.2 \pm 3.7$) was estimated to have been formed during 1936 to 1944 (Table 1).

The simulation of the three VBGF models resulted in a variable precision in their ability to estimate the date of formation of the subsample formed at 227 mm MSL. We assume this subsample to have been formed at 1959, the inception of the radiocarbon rise in the northeast Pacific. In order for the model with $L_\infty = 313$ mm MSL to predict this year of formation of the 227 mm MSL subsample, the value of the k in the model could not exceed 0.040 y^{-1}. For the model with $L_\infty = 298$ mm MSL to predict the year of formation of the 227 mm MSL subsample the value of k could not exceed 0.050 y^{-1}. In these two cases the expected value of k was outside the

predicted 95% confidence interval of the parameter. The value of k necessary for the model with L_∞ = 283 mm MSL to predict the date of formation of 1959 is 0.068 y^{-1} and this was the only model to precisely predict the date of formation of the 227 mm MSL subsample within the estimated 95% confidence interval of k (0.0673 to 0.0705 y^{-1}).

DISCUSSION

In this paper we show that red abalone shell material is a recorder of the regional temporal pattern of $\Delta^{14}C$; the temporal trend of $\Delta^{14}C$ levels measured in the abalone shell generally corresponded to both the yelloweye rockfish and Pacific halibut time series', and that the use of $\Delta^{14}C$ analysis of red abalone shell material can provide insight into the validity of VBGF estimates. We evaluated the fit of each candidate growth model with the tag-recapture data and in reference to its prediction of the year of the inception of the rise in radiocarbon. We found that the model that best described the tag-recapture data (the lowest AIC value) was the most reasonable at predicting the year of the subsample formed at the inception of the rise of radiocarbon in the northeast Pacific.

We conclude that the growth model with L_∞ = 283 mm MSL and k = 0.0689 y^{-1} (95% CI: 0.0673 to 0.0705 y^{-1}) provides the best fit of the three candidate models because this model predicts the date of formation of the critical 227 mm MSL subsample most precisely. It is unlikely that the 227 mm MSL subsample was formed in the early 1960's, as the two alternative growth models (L_∞ = 298 mm MSL and L_∞ = 313 mm MSL) predict because the corresponding VBGF growth rate constant (k y^{-1}) for each model would need to be very small ($\leq$ 0.040 or $\leq$ 0.050 y^{-1}). The age of this specimen, predicted from the best fit curve is not younger than 32 y and could be

1 older. We note that this conclusion does not preclude the validity of a model parameterized with a
2 value of L_∞ less than 283 mm MSL.

3 The temporal correspondence of $\Delta^{14}C$ and the estimated ages of each red abalone
4 subsample are similar to both of the regional time series' but there appears to be a slight shift
5 toward more recent years of formation. Ambiguity in the date of specimen collection could result
6 in this apparent shift: the uncertainty of ±1 y for the collection year can explain the shift in the
7 subsample series, if the shell was indeed collected in 1967. Because the subsample extracted at
8 249 mm was 2 mm away from the leading margin of growth it may have formed as early as 1966.
9 The measured $\Delta^{14}C$ level for this subsample, when compared to the reference time series, provides
10 support for this hypothesis. This subsample was important in the time series because it sets up the
11 basis for projecting growth back to a birth year: it was clearly formed after the inception of the ^{14}C
12 rise.

13 The VBGF parameters from the best fit model presented in this study are considerably
14 different than those previously reported for red abalone. Ault (1985), using red abalone collected
15 in northern California and maintained in aquaria, determined k values of 0.11 y^{-1} to 0.19 y^{-1}.
16 Rogers-Bennett et al. (2007) reported VBGF parameter values of $k = 0.108$ y^{-1} and $L_\infty = 254.2$ mm
17 derived from 208 recaptures at a single location in northern California and included 38 tagged
18 individuals that were 50 to 100 mm MSL when first tagged and were at liberty from eight to 16
19 months. A subset of 23 individuals in this data were 5 to 30 mm MSL at first tagging. The VBGF
20 estimates of the tag-recapture data used in this study, when analyzed using Fabens' method with an
21 unconstrained L_∞ parameter value, resulted in VBGF estimates of k that were more similar to these
22 published studies: $k = 0.159$ y^{-1} (95% CI: 0.150 to 0.168 y^{-1}) ($L_\infty = 201.470$ mm MSL, 95% CI:
23 198.1 to 204.9 mm MSL) than the values of k predicted in this study when L_∞ was constrained.

The differences between the k values reported in this work and those previously reported may be due to differences in the spatial and temporal growth dynamics of red abalone, the misspecification of VBGF model parameters, or misspecification of the von Bertalanffy growth model to describe the age-at-length relationship of this species in northern California. McShane et al. (1994) reported that significant differences in the mean length of *H. iris* populations in New Zealand are correlated to latitude and exposure. Variation in VBGF parameters among populations of *H. iris* are a result of differences in relative exposure (McShane & Naylor 1995) and it is likely that the fine scale variation in growth at different sites, which were combined in this study, has contributed to the low precision of the VBGF estimates. Temporal variation in growth trajectories of red abalone has been described in southern California by Haaker et al. (1998); it was suspected that growth is depressed during periods of increased water temperature and low productivity. Experimental work has supported this hypothesis (Vilchis et al. 2005). The misspecification of the arbitrarily chosen values of L_∞ may have also contributed to differences in the growth trajectories predicted by this and previously published studies: VBGF parameters k and L_∞ are strongly negatively correlated (Chen et al. 2003). The assignment of a large, arbitrary chosen L_∞ value will greatly influence the value of k. Finally, although the VBGF has been widely used to describe the age-at-length relationship of Haliotidae (Day & Fleming et al. 1992) it generally has a poor fit to abalone growth (Matsuishi et al. 1995) and alternative models have been used (Rogers-Bennett et al. 2007, Hancock 2004). The relatively consistent underestimation of growth of small (< 150 mm MSL) and overestimation of growth of large (> 150 mm MSL) red abalone observed in this study, as indicated by the vector method, may indicate that the VBGF may not be appropriate to describe the age-at-length relationship of this species in northern California (Figure 1).

Our work suggests that $\Delta^{14}C$ dating can be applied in a more comprehensive study to determine the ontogenetic growth trajectory of red abalone, guide growth model specification, and growth model parameter selection. We recognize that making population level inferences from four autocorrelated subsamples, taken from a single individual, implies numerous assumptions including: the single specimen grew in a similar way to all northern California abalone, that ^{14}C uptake is consistent throughout ontogeny, and that the age-at-length relationship derived from tag-recapture work from multiple sites from 1971 to 1978 is similar to that of the subsampled specimen collected in 1968 (± 1 y) which had an estimated birth year of 1936. A strategy that consists of intensively subsampling a number of large similar sized red abalone shells with known dates of collection from the same area is necessary for a complete and unambiguous age and growth validation for this species in the region. The results of this study indicate that such an approach is promising. Although the tag-recapture work used in this study approximates a growth rate that is plausible, analysis of ^{14}C allows for an alternate determination of growth rates and the determination of the maximum age of large individuals.

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Table 1. Summary of estimated ages, dates of formation, and $\Delta^{14}C‰$ for extracted samples.

Shell length at extraction (mm)	Estimated mean age and (range) years[i]	Estimated mean year and (range) of sample formation[ii]	Sample mass (mg)	$\Delta^{14}C‰$	±
249	31 (27 to 32)	1967 (1966 to 1968)	5.0	-16.8	4.8
227	24 (22 to 24)	1960 (1959 to 1963)	5.1	-93.2	4.2
217	21 (20 to 22)	1957 (1957 to 1961)	6.1	-104.0	3.6
75	4 (4 to 5)	1941 (1940 to 1945)	5.0	-115.2	3.7

i. The estimated mean age was derived from the mean parmater estimate of the best fit von Bertalanffy model (L_∞=283 mm MSL, k=0.0689 y^{-1}). The age range was derived from the absolute minimum and maximum age estimates of the three von Bertalanffy curves and incorporated the 95% confidence intervals of k of each curve and the width of the sample extraction (shell length at extraction ± 0.5 mm).

ii. The mean year of sample formation was derived from the mean age estimate and an assumed date of shell colleciton of 1968. The range in year of sample formation was derived from the estimated range of ages and incorporated the variation in the estimated date of collection of the shell (1968 ± 1 year).

Figure legends

Figure 1.

Tag-recapture growth vectors fit to the best fit Von Bertalanffy growth function (k = 0.0689 y^{-1}, L_∞ = 283 mm MSL). Growth vectors are anchored to the curve by assuming that the age at tagging is predicted by the VBGF. Vectors represent growth as the change in maximum shell length (ΔMSL, mm) during time between tagging and recapture (Δ years).

Figure 2.

Radiocarbon values of red abalone subsamples extracted from a single individual in relation to their estimated mean formation dates based on the best fit von Bertalanffy growth curve (k = 0.0689 y^{-1}, L_∞ = 283 mm MSL) and two reference time series: southeast Alaska yelloweye rockfish (Kerr et al. 2004) and northeastern Pacific halibut (Piner and Wischniowski 2004).

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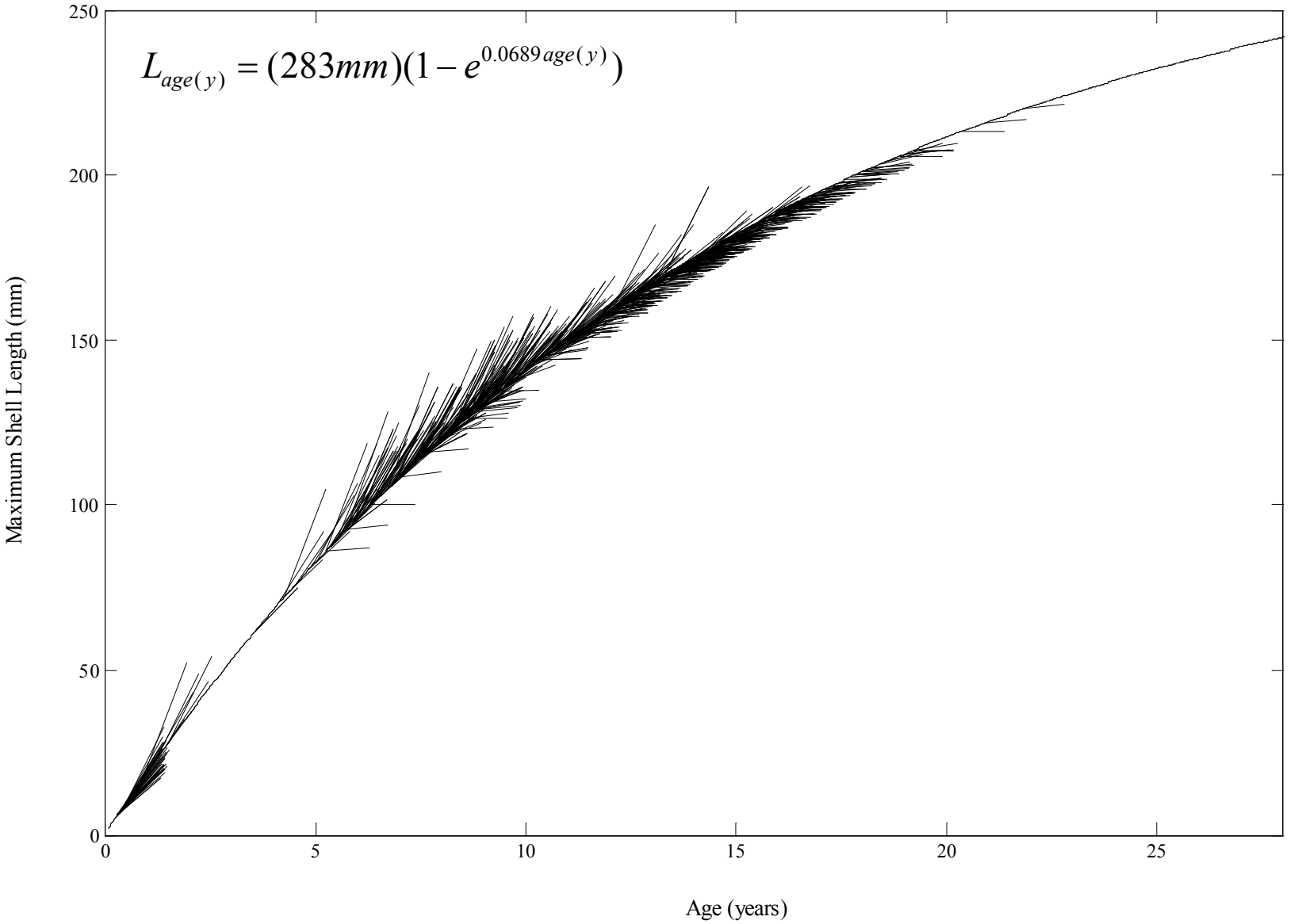
Figure 1.



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